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Advancing research on alien species and biological invasions

Some reflections on current invasion science and perspectives for an exciting future

Tina Heger[1,2,3,4,5], Jonathan M. Jeschke[2,4,5], Johannes Kollmann[3,6]

1 *University of Potsdam, Biodiversity Research / Botany, Maulbeerallee 2a, 14469 Potsdam, Germany* **2** *Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Königin-Luise-Str. 2–4, 14195 Berlin, Germany* **3** *Restoration Ecology, School of Life Sciences, Technical University of Munich, Emil-Ramann-Str. 6, 85354 Freising, Germany* **4** *Freie Universität Berlin, Institute of Biology, Königin-Luise-Str. 1–3, 14195 Berlin, Germany* **5** *Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Müggelseedamm 310, 12587 Berlin, Germany* **6** *Norwegian Institute for Bioeconomy Research (NIBIO), Postboks 115, 1431 Ås, Norway*

Corresponding author: Tina Heger (t.heger@wzw.tum.de)

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Abstract

Species spreading beyond their native ranges are important study objects in ecology and environmental sciences and research on biological invasions is thriving. Along with an increase in the number of publications, the research field is experiencing an increase in the diversity of methods applied and questions asked. This development has facilitated an upsurge in information on invasions, but it also creates conceptual and practical challenges. To provide more transparency on which kind of research is actually done in the field, the distinction between invasion science, encompassing the full spectrum of studies on biological invasions and the sub-field of invasion biology, studying patterns and mechanisms of species invasions with a focus on biological research questions, can be useful. Although covering a smaller range of topics, invasion biology today still is the driving force in invasion science and we discuss challenges stemming from its embeddedness in the social context. Invasion biology consists of the building blocks 'theory', 'case studies' and 'application', where theory takes the form of conceptual frameworks, major hypotheses and statistical generalisations. Referencing recent work in philosophy of science, we argue that invasion biology, like other biological or ecological disciplines, does not rely on the development of an all-encompassing theory in order to be efficient. We suggest, however, that theory development is nonetheless necessary and propose improvements. Recent advances in data visualisation, machine learning and semantic modelling are providing opportunities for enhancing knowledge management and presentation and we suggest that invasion science should use these to transform its ways of publishing, archiving and visualising research. Along with a stronger focus on studies going beyond purely biological questions, this would facilitate the efficient prevention and management of biological invasions.

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Keywords
biological invasions; evidence-based management; grand unified theory; invasion science; open science; philosophy of science; social-ecological systems; theory development

Introduction

During biological invasions, organisms spread and establish outside their native range. These processes are investigated in a vibrant and still-growing research field, with the number of papers published in specific outlets, as well as in general ecological journals having increased exponentially during the past decades (Vaz et al. 2017; Cassey et al. 2018). Reasons for studying biological invasions are manifold. Invasive species are amongst the five most significant global drivers of biodiversity loss (IPBES 2019). Applied research is thus needed to deliver guidance for how to prevent further invasions and how to manage invasive species, where necessary. At the same time, biological invasions are highly interesting study objects, because they represent 'natural experiments', allowing the study of how species respond to novel biotic interactions and environmental conditions. Research in this field is challenging for many reasons, including the high complexity of factors influencing the process, amongst them ecological and evolutionary as well as social-economic feedbacks (Heger et al. 2013; Courchamp et al. 2016).

Several times, it has been questioned whether 'invasion biology' should be addressed as a discipline at all, the main argument being that the process of invasion does not fundamentally differ from other ecological processes as, for example, colonisation (e.g. Davis 2009; Valéry et al. 2013). In line with Blondel et al. (2014), we suggest that the ongoing increase in publications on biological invasions clearly demonstrates that a broad community of researchers disagrees with this argument and, actually, the field still grows and makes substantial progress (see, for example, Hui and Richardson 2017; Vaz et al. 2017; Wilson et al. 2020). In addition, the topic of biological invasions is central to biodiversity conservation (IPBES 2019) and has become an integral part of international policy (e.g. European Union 2014), underlining the societal need for a scientific discipline dedicated to it.

Due to the diversity of reasons for studying the phenomenon, as well as the high complexity of influencing factors, biological invasions are investigated in a multitude of different ways. This has substantially increased our knowledge about invasive species and their impacts, while the expansion of the field increasingly creates conceptual and practical challenges. For example, it is nearly impossible to keep track of all case studies that are published on the patterns and processes of biological invasions and improved efforts are needed to ensure that individual results become integrated into the body of theory (Jeschke and Heger 2018a). Given the breadth of topics and approaches and the rate at which new publications accumulate, gaining an overview of the field or even on the state of knowledge in some more specific sub-field is becoming difficult.

In light of these challenges, we suggest three topics that, from our point of view, need further consideration. First, we discuss the delineation of the field, recalling the

previously-proposed distinction between 'invasion science' and 'invasion biology'. Second, we will discuss the structure of invasion biology and ask whether, given the increasing breadth and diversity of the field, there is a need for a unified theoretical framework. We will draw from recent publications in philosophy of science and argue that invasion biology may be a well-functioning discipline without one grand unifying theory, but that more integration, nevertheless, is desirable. Third, we will suggest future steps that could be taken to reach such integration, given the ongoing rapid technological advances and the current changes in the processes involved in scientific publication.

Invasion biology and invasion science

Research at the interface between nature and society

As one of many problem-orientated disciplines, invasion biology, just like ecology in general, is located at the intersection between nature and society (Fig. 1) and thus encompasses basic as well as applied research. In a review of 500 studies published in 2008, a large proportion (74%) covered basic ecological questions and had a focus on community ecology, biogeography, population biology, evolutionary biology or molecular ecology (Richardson 2011). Such studies aim at a mechanistic understanding of patterns and processes and can be classified as generating 'systems knowledge' (Richardson 2011, with reference to Kueffer and Hirsch Hadorn 2008). The high percentage of remaining studies in the dataset, however, focuses on the phenomenon of biological invasions from an applied perspective. In this sample, 14% of the studies aimed at clarifying conflicts of interest and values and perception of people ('target knowledge', Kueffer and Hirsch Hadorn 2008; Richardson 2011). These were, for example, studies on risk assessment or from the fields of environmental ethics or resource economics. The remaining publications in the dataset aimed at finding appropriate actions for management ('transformation knowledge'), stemming, for example, from restoration ecology.

Studies creating target knowledge and transformation knowledge are clearly outside the realm of ecology as a natural science. Consequently, Richardson (2011) suggested distinguishing between 'invasion ecology' as the "study of causes and consequences of the introduction of organisms to areas outside their native range" and 'invasion science', describing the "full spectrum of fields of enquiry that address issues pertaining to alien species and biological invasions" (Richardson et al. 2011). The term 'invasion ecology' is often used interchangeably with 'invasion biology'. We regard ecology as a sub-discipline of biology and, therefore, prefer 'invasion biology' as the broader term, explicitly including, for example, evolutionary and genetic topics as well.

In the following, we will argue that the distinction between invasion biology and invasion science can still be helpful today, as it stresses the difference between studies focusing on biological research questions and other fields of enquiry. It can, thus, contribute to more transparency concerning which kind of research is actually done in the field and thus has the potential to enhance the diversity of research approaches.

Invasion science: biological invasions as processes affecting and effected by social-ecological systems

For a long time in ecology and biological conservation, humans have been treated as apart from natural processes (Mace 2014; Inkpen 2017). During the past decades, however, this mindset has largely changed. Today, ecology is no longer focused on studying only systems 'untouched' by humans, but instead, sub-disciplines are thriving that explicitly focus on ecosystems influenced by humans, like urban ecology, global change ecology or indeed invasion biology. Conservation today focuses on 'people and nature' (Mace 2014) and relational approaches to environmental ethics are gaining momentum as well (Chan et al. 2016; Eser 2016; Klain et al. 2017; Himes and Muraca 2018). Consequently, an increasing number of authors call for more explicit consideration of the effects of society on patterns and processes in nature and the creation of closer links between ecological and social sciences (e.g. Díaz et al. 2015; Ellis 2015; Perring et al. 2015). In the Anthropocene, human activities affect every ecosystem and it is argued that, in order to understand current ecological patterns and processes, the environment has to be viewed and studied as coupled social-economic and ecological systems (Ostrom 2009; Collins et al. 2011).

Biological invasions are providing prime examples for the multiple ways in which ecological processes and human activities are influencing each other (McNeely 2001; Kueffer 2017). Social-economic activities are strongly affecting invasion processes in many ways and only since this crucial fact has been taken into account (see, for example, Hulme 2009) has it become possible to develop efficient measures for preventing and managing invasions, for example, by tackling major introduction pathways. In an encompassing literature review, Vaz et al. (2017) demonstrate that publications on biological invasions formerly used to report purely ecological research, but since the 1990s and 2000s, social and socio-ecological research on biological invasions has gained importance.

Connections to social sciences are, for example, sought with the aim to enhance the process of evaluating invasive species (e.g. Bacher et al. 2018; Shackleton et al. 2018). Interdisciplinary teams are formed, for example, to study the spread of acacias, taking into account not only ecological, but also historical, political, ethical and aesthetic aspects (Carruthers et al. 2011).

Moreover, several authors meanwhile made concrete suggestions for addressing biological invasions as processes happening within social-ecological systems. Drawing from methods developed in complexity science, Hui and Richardson (2017) explore how invasion science could profit from treating invasion syndromes as complex adaptive systems – as "dynamic systems comprising multiple interacting parts that can adaptively and collectively respond to perturbations" (p. 268). Here, human beings and their agency are considered part of a network and this method would allow taking into account the complex interactions and feedback loops tying together invading species, invaded ecosystems and social-economic systems. In a similar way, Sinclair et al. (2020) suggest subdividing the invasion process into three 'coupled human and natural systems' (CHANS), each describing a specific feedback loop interlinking the fate of invading organisms with human activities during specific sections of the invasion process.

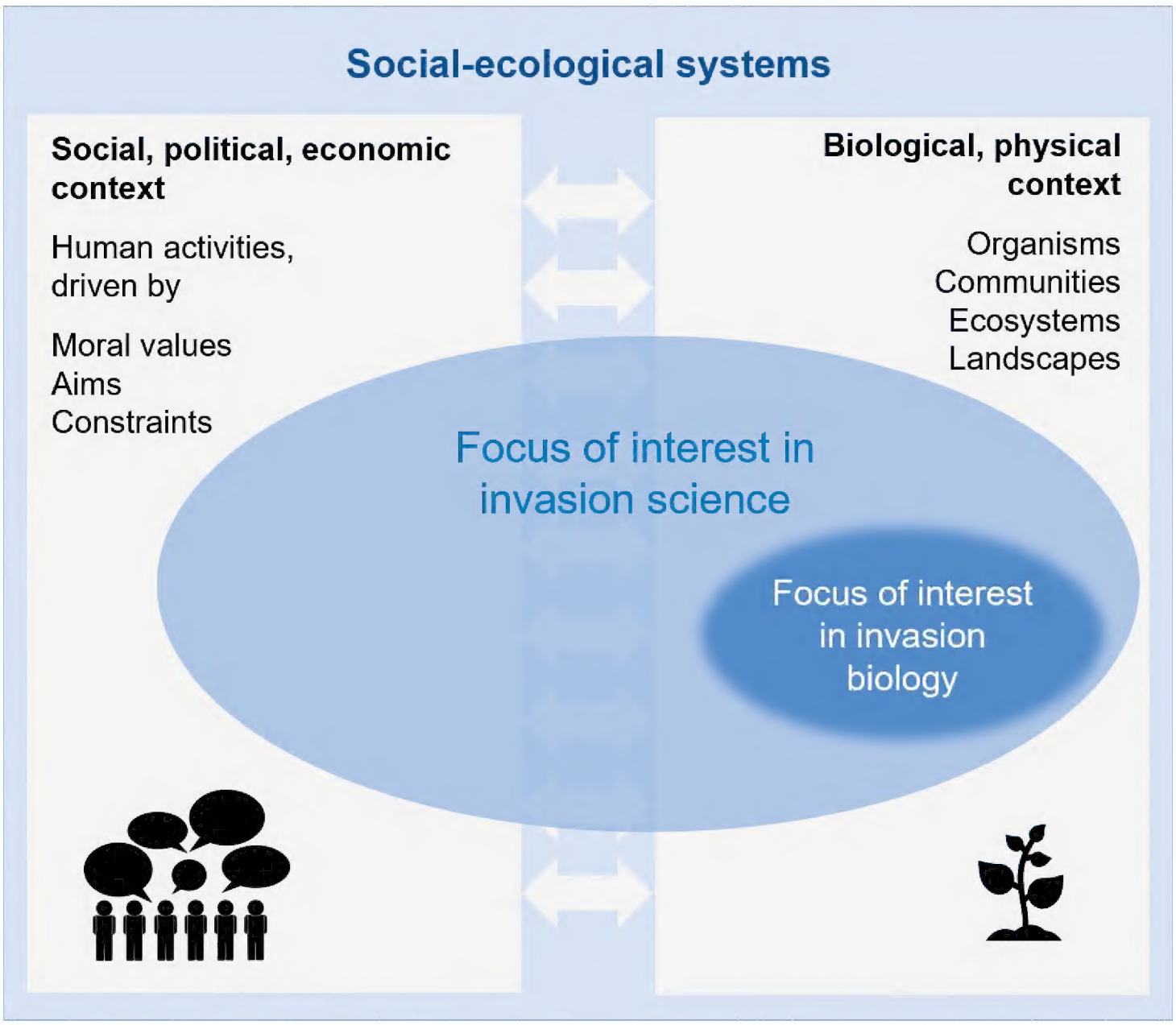

Figure 1. Research on biological invasions is located at the intersection between natural sciences (biological and physical context) and the social sciences and humanities (social, political and economic context). The concept of 'social-ecological systems' (outer light blue box) emphasises that both realms are closely connected, with human activities affecting organisms, communities, ecosystems and landscapes and vice versa. Invasion biology addresses biological questions about patterns and mechanisms of invasions and, thus, has a focal interest in the biological and physical context. The broader field of invasion science contains research analysing patterns and mechanisms of invasions from a social-economic point of view, effects of invaders on people's values and perspectives and many other, non-biological aspects of species invasions.

To give a more concrete example, Ferreira-Rodríguez et al. (2019) applied the interdisciplinary and integrative social-ecological systems framework developed by Ostrom (2009) to analyse the introduction and dispersal of Asian clam *Corbicula fluminea* in Spain. This framework uses a combination of methods from natural sciences (i.e. sampling water bodies) and the humanities (semi-structured interviews) and considers social, ecological, economic and governance subsystems. This way, the authors are able to demonstrate that the distribution of the Asian clam is statistically related, not only to ecological factors as, for example, water temperature, but also to socio-economic variables like education level, the industrial productivity index and the number of NGOs in the region. These findings may help to adjust management and policy actions.

Approaches like these, leaving the realm of pure ecological or biological research, are promising and might be the best choice, especially for finding ways to prevent and manage invasions. However, with their literature review, Vaz et al. (2017) found that, out of more than 9,000 publications addressing biological invasions since the 1950s, 92.4% focused on purely ecological questions. A potential reason for this observation is that research crossing disciplinary boundaries is challenging and there is a lack of regular interaction of the respective peer groups. This is an observation not only made by social-ecological scientists (Ostrom 2009), but also by philosophers: Millgram (2015) argues, for example, that we are living in an age of 'hyperspecialization' and everyone outside of their own field of expertise tends to be a logical alien. Specifically, we are not familiar with the standards and procedures of neighbouring fields and guidance is usually missing on how to apply methods we are not trained to use, how to interpret data that take different forms than we are used to and how to assess results derived with these methods and data (see also Jeschke et al. 2019b). Therefore, a current challenge of invasion science is to increase efforts in overcoming these boundaries and to develop into a truly interdisciplinary field.

Invasion biology: natural science embedded in a societal context

The usefulness and necessity of interdisciplinary studies does not preclude the need for studies focusing on biological research questions (Collins et al. 2011). Basic ecological and evolutionary mechanisms underlying the establishment and spread of species need to be better understood to allow accurate predictions and more efficient management, including the importance of species interactions in hindering establishment or the effects of novel interactions on trait evolution; this is the core of invasion biology (Fig. 1). Richardson et al. (2011) originally defined invasion science as the "full spectrum of fields of enquiry that address issues pertaining to alien species and biological invasions" and invasion biology as the "study of causes and consequences of the introduction of organisms to areas outside their native range". Many significant causes and consequences, however, are closely linked to the societal, political and economic context. We suggest that instead, invasion biology could be defined as the study of patterns and mechanisms of species invasions with a focus on biological research questions. Invasion science is the overarching research area that includes invasion biology and, additionally, amongst others, the study of species invasions as social-ecological phenomena, focusing on social, political and economic processes and their interactions with biological invasions. The broad discipline of invasion science can and should involve the integration of knowledge and methods developed in non-biological disciplines (Fig. 1).

Invasion biology in this sense is studying organisms, communities, ecosystems, landscapes and biomes, typically with a focus on ecological and evolutionary questions. It aims, for example, at explaining how invaders change species interaction networks or at predicting which species compositions increase the probability for invasion. Human activities are important here because their effects on the biophysical context are nearly ubiquitous and, thus, are inseparable parts of the study objects. For answering a biologi-

cal question (for example, about the interaction of two species), however, it is not necessary to study human activities themselves nor their causes (see also Gounand et al. 2018). With its focus on biological research questions, invasion biology usually does not need to directly incorporate knowledge and methods from the social sciences or humanities.

Nevertheless, invasion biology still is embedded in a social context (Fig. 2) – it is affected by and has effects on society. For example, the social context of a study (e.g. country, lab, knowledge of the principal investigator) influences the research focus, the choice of the study system and methods, as well as the focus of analyses, communication of results and decisions to take management action (inward blue arrows in Fig. 2) (see, for example, Schurz 2014, p. 41–44). Conversely, the outcomes of scientific studies affect opinions and decisions, within invasion biology as well as in society at large (outward blue arrows in Fig. 2).

This embeddedness of invasion biology in a societal context leads to complex relationships between facts and values (Justus 2013). Biological research on invasions is often linked to societal values and goals (Backstrom et al. 2018). This can be problematic, as a common conception of good scientific practice posits that science should be performed objectively. Scientific research should only describe the facts as observed, while deriving value judgements (i.e. a situation is good or bad) or normative claims (i.e. an action is right or wrong) is outside the realm of scientific practice. It is known from philosophy of science that, during the planning of a research project, as well as during the subsequent phase of utilising the results, it cannot be avoided that value assumptions stemming from society have an effect. In invasion biology, for example, researchers prefer studying those species with a strong impact over those that have less impact (Pyšek et al. 2008). Such societal influences create biases that need to be accounted for; but the respective studies themselves can nevertheless represent sound and solid science. During the phases of generating and testing hypotheses and gathering data (i.e. the context of justification), care has, thus, to be taken to avoid that fundamental value assumptions influence the process (Schurz 2014). Otherwise, a statistical negative correlation between the number of native and alien species could, for example, be misinterpreted, leading to false conclusions about underlying causes of observed patterns.

The influence of implicit values on research in invasion biology has been discussed within the discipline (e.g. Larson 2005; Colautti and Richardson 2009). Still, the challenge persists and, for instance, a recent literature survey showed that invasion biology uses militaristic language more frequently than research on other topics in ecology and conservation biology (Janovsky and Larson 2019). Given this observation, it is comforting that, in philosophy of science, there are alternative opinions as well, suggesting that, especially in disciplines driven by ethically relevant questions, values and facts are so closely intertwined that a proper separation is not possible (see Justus 2013 for a review of this discussion). However, we believe there is no question that, in invasion biology, the ideal of objectivity should be pursued during data gathering, analysis and interpretation.

The relationship of invasion science and invasion biology as sketched in Fig. 1 suggests that, given the much broader coverage of invasion science, the majority of

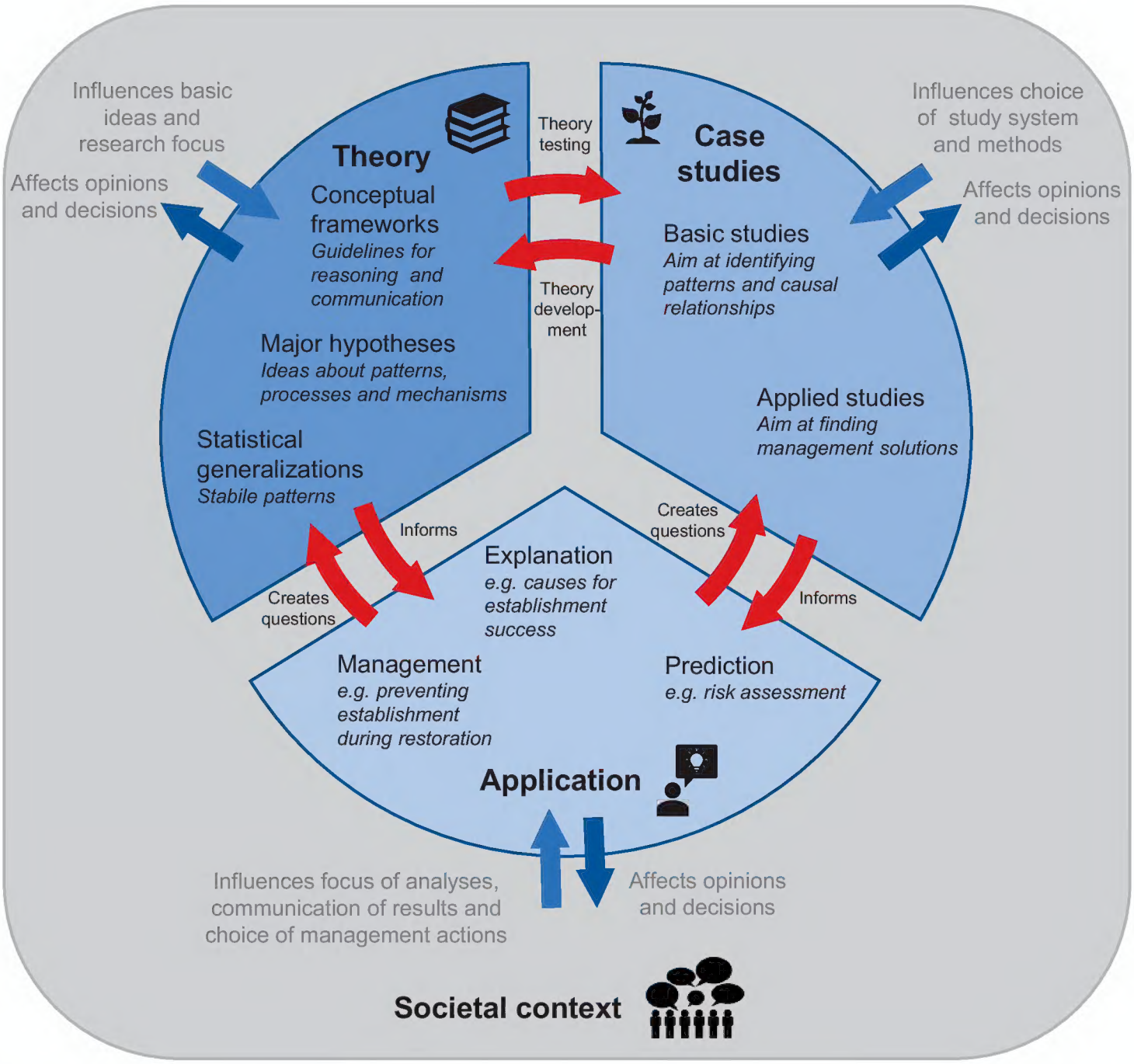

Figure 2. Invasion biology, with its building blocks theory, cases studies and application, is embedded in a societal context. The red arrows show how theory, case studies and application affect each other; the blue arrows depict effects of society on invasion biology and vice versa. The lighter colour of the block 'application' indicates that also non-biological questions beyond invasion biology, as defined above, are addressed here – these are part of invasion science (see Fig. 1).

studies in this field should lie outside of the narrow range of topics covered by invasion biology. The results of Vaz et al. (2017), however, demonstrate the opposite. We agree with Vaz et al. (2017), Hui and Richardson (2017) and others that invasion science can profit from focusing research much more on questions outside of invasion biology. Embracing approaches like network theory (see also Frost et al. 2019) or complex adaptive system modelling and framing invasions from a social-ecological perspective, could strongly aid explanation, prediction and management of invasions. However, we also think that it is useful to keep in mind that there is and, probably, always will be, a sub-field in invasion science that focuses on basic biological research questions and that the broad field of invasion science can profit from such studies as well. Given that invasion biology still represents the core of invasion science, we will now take a closer look at this field.

The role of theory in invasion biology

The structure of invasion biology

A major building block of invasion biology is theory, consisting of conceptual frameworks, statistical generalisations and major hypotheses (Fig. 2). Two other important building blocks are case studies and applications. Being an empirical natural science, the discipline relies on observations and experiments; case studies, therefore, are indispensable elements, delivering a broad and solid basis for knowledge gain. Most publications in invasion biology report on such case studies, i.e. evidence collected in field surveys, common gardens, greenhouses or lab facilities or based on mathematical models (which often are also part of theory). They can either have the aim to identify patterns and causal relationships, thus contributing to answering basic questions or they can aim at identifying management solutions.

According to a classic idea of scientific progress, the main purpose of cases studies is to test specific elements of theory. Indeed, many studies in invasion biology do so, i.e. they test ideas that are grounded in theory (Fig. 2). A prime example are studies that test specific hypotheses in invasion biology (see Jeschke and Heger 2018a), as, for example, the enemy release hypothesis. However, case studies do not regularly test single well-defined hypotheses or other elements of theory. This is a fact that has been noticed by philosophers of science for other parts of biology as well. For example, Elliott (2019) observed that research often focuses on addressing problems (for instance, species X invades a community containing endangered species) rather than testing theory (see also Love 2008) and each research problem can invoke a range of research questions. This conception of science seems to be well in line with the practices of invasion biology and philosophical studies indicate that research directed at addressing problems is not scientifically inferior to research testing hypotheses or other elements of theory.

The knowledge gained in case studies and through theory development can be applied in various ways. With respect to invasion biology, application can mean to use the knowledge for preventing and managing species invasion. In addition to such practical application, new knowledge can be used for prediction and explanation. Explanation is often an implicit part of case studies. An empirical project typically starts with a question or hypothesis, conducts an experiment or survey, analyses the data and then uses the results to explain the observed patterns in the light of theory. If multiple case studies are synthesised, the aim usually is to find explanations that are more broadly applicable; and ideally, these can be used to derive predictions by extrapolating or transferring the insight to other situations.

The abovementioned building blocks (theory, case studies, application) can be linked in various ways (red arrows in Fig. 2): theory and case studies can deliver the knowledge base for application and the three forms of application (explanation, prediction, management) can deliver questions that generate the motivation to perform case studies and develop theory. Theory creates research questions and elements of theory can be empirically tested in case studies. On the other hand, the insight gained from case studies can be used to develop theory.

Is there a need for a grand unified theory of invasion biology?

Theory in invasion biology can take the form of conceptual frameworks, statistical generalisations and major hypotheses (Fig. 2). A recent special issue in this journal provides an overview of conceptual frameworks that are being used in invasion science (Wilson et al. 2020). The 24 contributions demonstrate the usefulness of these elements of theory for research, policy and management. Other work has demonstrated the richness of major hypotheses formulated in invasion biology and has made efforts to show the level of empirical support and their connectedness (Jeschke and Heger 2018a; Enders et al. 2020; Jeschke et al. 2020). These efforts underline that the discipline contains and is based on a well-developed body of theory. It may be asked, however, whether this theory is sufficiently well integrated. The term 'theory' is often used to describe a concise, unified, general framework, analogously to the 'grand unified theory' in particle physics that provides a strong knowledge base in a research field. The question is whether invasion biology has, or will ever have, such a kind of theoretical basis.

In the late 20th century, ecology picked up physics as a role model (Trepl 1987) and philosophy of science commonly praised this discipline as the prime example of how to conduct scientific research. Consequently, the claim was that every proper branch of science should strive for developing a grand unified theory. However, it became increasingly obvious that not all scientific disciplines can be compared to physics and that the development of a grand unified theory may not be a common goal. In philosophy of science, an argument is gaining momentum which posits that, in the so-called special sciences, such as biology, the high complexity of the study objects and high context-dependency of processes make the search for universal laws and a unified theory difficult or even impossible (Reutlinger et al. 2019) and that a discipline can very well produce fruitful results without having a unified theory (Love 2014).

Invasion biology seems to be such a discipline. It does not have one concise unified theoretical framework, but is still based on a substantial body of theory (see, for example, Catford et al. 2009; Enders et al. 2020; Wilson et al. 2020). The absence of a unified theory that can comprehensively explain the phenomenon of invasion and guide research has been regarded as a deficiency of the field by invasion biologists, as well as critics of the discipline (see, for example, Richardson et al. 2008) and there have been calls for developing a "broadly applicable conceptual framework grounded in basic principles of ecology and evolutionary biology" (Gurevitch et al. 2011, p. 407). From recent philosophical studies, we conclude, however, that the search for a unified theory, for 'basic principles' or for an extensive explanatory framework is probably not the most efficient way forward for invasion biology (Love 2014; Elliott-Graves 2016). Theory here, as well as in ecology in general, can rather be viewed as an "ever-changing, context-dependent, collective construct" (Travassos-Britto et al. 2021b) and, as such, is suited well to guide research and build knowledge. Striving for extensive synthesis, by contrast, carries the danger of over-generalisation and of sacrificing too many of the details that are required for truly enhancing explanation, prediction and management (Elliott-Graves 2016).

Even if we conclude that the search for a unified general theory is not a useful aim for invasion biology, this does not mean that integration and synthesis is useless. We suggest the opposite: invasion biology needs more integration and synthesis. The aim, however, should not be to strive for a single general framework or (mathematical) theory that explains everything, but to explore novel ways for integration that allow for plurality and consider the context-dependency of invasions.

The development and harmonisation of conceptual frameworks seems to be a useful way forward. Frameworks have the aim to organise knowledge and can function as guidelines for research and communication. Notably, most of the established frameworks in invasion biology have a focus on classification and description, often in a management context. For example, of the 24 papers included in the already-mentioned special issue (Wilson et al. 2020), only five discuss frameworks with regards to causes and mechanisms of invasions (Hulme et al. 2020; Liebhold et al. 2020; Pyšek et al. 2020; Robinson et al. 2020; Sinclair et al. 2020). This seems to demonstrate that the focus of theory development in the field currently is on producing knowledge useful for application. We suggest that, in order to improve the mechanistic understanding of biological invasions, it is important to foster the development and harmonisation of frameworks addressing causes and mechanisms of invasions as well.

In addition, we believe that invasion biology could profit from a more explicit consideration of how knowledge is generated and from systematically analysing its conceptual basis (see suggestions in Travassos-Britto et al. 2021a; Travassos-Britto et al. 2021b for ecology). Further philosophical analyses of the research practices in invasion biology could help to identify weaknesses in current methods and strategies and could, thus, facilitate methodological improvement. There is a rising interest of philosophers of science in ecology and also invasion biology (e.g. papers cited here and Elliott-Graves 2016; Bausman 2019; Elliott-Graves 2020; Justus 2021) and we should seize this opportunity to build sustainable collaboration, based on an interdisciplinary research agenda, involving invasion biologists and philosophers.

The future of invasion science: opportunities abound

Evidence-based management

A multitude of different methods, ranging from field surveys and experiments to molecular studies and mathematical models are used to address various basic and applied questions in invasion biology. The majority of studies in invasion biology focus on terrestrial plants (Pyšek et al. 2008; Jeschke and Heger 2018b), but even within this group, research approaches are quite diverse. This diversity is necessary to address the entire range of invasion cases and processes involved. It creates the challenge, however, how this wealth of information can be efficiently used for improving theoretical foundations and practical applications.

In ecology, there have been several initiatives to synthesise evidence from empirical studies to allow for efficient, evidence-based conservation (www.conservationevidence.com) and environmental management (www.environmentalevidence.org; see also www.eklipse-mechanism.eu and Nesshöver et al. (2016)). Studies contributing to these initiatives provide guidance for policy decisions and local management and favoured tools are, for example, systematic reviews and statistical meta-analyses, following specific protocols. Species invasions are one out of many topics addressed in these initiatives, but are currently the focus of relatively few synthesis studies; for example, only six systematic reviews out of more than one hundred at www.environmentalevidence.org (search date: 17 May 2021). Systematic reviews and meta-analyses are regularly undertaken in invasion biology, but such studies rarely aim at evidence-based management. A notable exception is the ongoing IPBES assessment on invasive alien species. It is possible that a limited awareness of evidence-based conservation portals in invasion biology or a lack of awareness of meta-analytical methods in researchers interested in application are reasons for this shortcoming. Evidence-based management has much potential for invasion biology and we urgently suggest a more regular use of the available tools and platforms. The management of invasive species is a dynamic research field, as exemplified by the successful bi-annual 'Conference on Ecology and Management of Alien Plant Invasions' (EMAPI) (Pyšek et al. 2019). Making evidence-based management a prominent approach in this field would, for sure, increase the chances for efficient prevention and mitigation.

Enhancing research in the broader field of invasion science

Evidence-based invasion management would become an even more promising approach if human-environment interactions were a regular research topic in invasion science. Modelling invasion syndromes as adaptive cycles or as complex networks including humans as actors has a strong potential to enhance predictability in invasion science (Hui and Richardson 2017). The development and implementation of efficient management, on the other hand, could profit from close cooperation with diverse stakeholders right from the onset (including the design) of a study. This aim could be reached by establishing long-term and reciprocal interactions of invasion scientists and diverse stakeholders (Vaz et al. 2017).

A significant increase in interdisciplinary research is needed, as invasion biological studies with a focus on biological questions will not suffice for facing the diverse challenges posed by biological invasions. Vaz et al. (2017), therefore, suggest the formation of "research teams comprising a balanced pool of social scientists (including scholars from the humanities) and ecologists (and other natural scientists)". We agree with this prospect.

Efficient theory development

A more philosophical, general problem is how to utilise empirical results for theory development. As indicated above, case studies are not necessarily linked to a specific

element of theory, but even if they are, their interpretation is not always straightforward. Is a single negative test result sufficient to discard an entire major hypothesis? According to an interpretation of the 'hypothetico-deductive method' based on Popper (1935), which is still rather prominent in ecology (e.g. Farji-Brener and Amador-Vargas 2014), discarding the hypothesis would, indeed, be the best option. Actual practice in ecology, as well as contemporary opinions in philosophy of science, however, do not follow such a strict approach of naïve falsificationism (Andersen and Hepburn 2016). It is a standard requirement for every scientific study that results are carefully discussed, considering results of studies performed in other systems or with different methods. A single negative result will, therefore, usually not be used as an argument to discard a major hypothesis in its entirety. Additionally, it is a standard problem for invasion biologists (and ecologists in general) that empirical studies deliver mixed results. Systematic reviews and statistical meta-analyses are used to deal with these challenges; they require, however, a minimum amount of methodological homogeneity that is not always given in a focal set of empirical studies and can have other challenges (de Vrieze 2018; Heger and Jeschke 2018b).

In addition to methodological heterogeneity, a challenge for synthesising the results of single cases studies is the high complexity of potentially relevant factors driving observed patterns. In the past, a general strategy to deal with the high complexity of interacting factors has been to focus on single factors. Explanation, prediction and management, however, will certainly profit from including more complexity. Respective suggestions have been repeatedly made in invasion biology (e.g. Heger 2001; Pyšek et al. 2020). We suggest that research at the interface of invasion biology, ecology and philosophy of science is needed to improve and implement these ideas and to develop further novel, innovative approaches for efficient theory development that considers complexity (e.g. Heger and Jeschke 2018a; Heger et al. 2021; Schurz 2021). Methods and tools are needed that explicitly consider what has been called 'causal heterogeneity' in philosophy of science, i.e. the fact that, in invasions, ecological entities can have different ways of causing invasions, depending on the situation (Elliott-Graves 2016). A promising way forward could be to defer the search for general patterns and mechanisms that can be found across systems and situations and, instead, focus on how the results of case studies could be used to delineate classes of cases in which there is causal homogeneity and where similar mechanisms apply. This approach could offer a way to balance the need for integration and synthesis with the necessity to account for complexity. Novoa et al. (2020) recently suggested the systematic identification of invasion syndromes, which they define as "a combination of pathways, alien species traits and characteristics of the recipient ecosystem which collectively result in predictable dynamics and impacts and that can be managed effectively using specific policy and management actions". Such a search for recurring patterns could indeed foster the establishment of effective management priorities.

It could be highly rewarding to additionally develop methods that allow for the identification of recurring causal patterns, thus fostering improved possibilities for mechanistic explanations. Parreño et al. (2021), for example, recently suggested a novel

meta-analytical method for identifying persistent causal relationships. They took information on the statistical analyses used in a set of biodiversity-productivity studies to infer (backwards) which causal relationships the respective studies have hypothesised. Thus, they identified commonly addressed hypothetical causal relationships, i.e. recurring patterns of hypotheses about causes. They concluded that, so far, data were still too sparse to allow for conclusions on actual recurring causal patterns on biodiversity-productivity relationships; but this method is a promising way forward.

Theory development could also be enhanced by fostering closer connection amongst fragmented elements of theory. For example, it has been suggested to demonstrate links and overlaps of established invasion frameworks by arranging them in a hierarchical way, thus creating a 'hierarchy of invasion frameworks' (Wilson et al. 2020). Ideally, the resulting structure would not only be published as a figure in a publication, but also as an interactive online tool, thus utilising advances in computer sciences and related fields (cf. https://hi-knowledge.org/). Novel developments in various research areas, including network theory (Hui and Richardson 2019), statistics and computer science (e.g. open access data aggregation, machine learning, semantic modelling), are being increasingly utilised in ecology (Algergawy et al. 2020; Heberling et al. 2021). We suggest, however, that much more potential lies in these advances and even more effort should be made to harness these developments for invasion science.

Enhanced knowledge management and presentation

Technological advances in computer science in addition provide innovative tools for visualising knowledge (Börner 2014; Kraker et al. 2016). For obtaining a first overview of a research field, the traditional approach is to search for textbooks summarising the state of knowledge or to use search engines like Google Scholar, Web of Science or Scopus. Textbooks, however, are outdated quickly and often do not perfectly match the specific interests of researchers. The existing scientific search engines deliver up-to-date information and can be adjusted to users' specific needs; to process their output, however, is a challenging and time-consuming effort. In addition, the more professional services are usually behind a paywall, hindering research for those without access to these services.

An openly-accessible, searchable knowledge base for invasion biology that provides search outputs in an intuitively structured way would, therefore, be a major achievement (Jeschke et al. 2021). Ideally, this tool would allow customised searches and interactive displays of search results, with direct links to the respective publications and underlying data. There is a growing number of databases in the field of invasion science, for example, the Global Invasive Species Database (http://www.iucngisd.org/gisd/), the Global Naturalized Alien Flora database (https://glonaf.org/), the Global Alien Species First Record Database (https://dataportal.senckenberg.de/dataset/global-alien-species-first-record-database) or the European Alien Species Information Network (https://easin.jrc.ec.europa.eu/easin) (see also Essl et al. 2015). These services provide valuable data on specific alien species and are a very good basis for comparative analyses. We suggest that, in addition, online tools are needed that provide an overview

of the field and deliver theoretical background information; they should also provide information about which major research questions and hypotheses have been empirically addressed for which taxonomic groups and realms and to what degree hypotheses have received empirical support. A tool that could deliver such kind of information is not necessarily an idealistic vision that will never be realised. First suggestions, making use of advances in data visualisation, machine learning and semantic modelling, are already being developed (Jeschke et al. 2021).

In addition to the recent technological advances providing the respective technical possibilities, the ongoing shift in scientific publication practices could also turn out to be facilitative for developing such tools. Calls for openly-accessible data and publications are gaining momentum (Wilkinson et al. 2016; Jeschke et al. 2019a) and services like pre-print servers and public data archives are added to the traditional portfolio of scientific work output. The traditional way of publishing results as a journal paper are increasingly supplemented by other approaches (see Auer 2019). Instead of sifting through high numbers of PDFs for finding those studies that match a certain research question, invasion scientists in the future should be able to utilise powerful tools like knowledge graphs, in which smartly developed algorithms collate the available information in visually appealing and easily understandable ways.

In conclusion, we believe that exciting developments are under way and we hope that our contribution stimulates efforts to seize these upcoming opportunities. Respective projects would require teaming up with experts from other disciplines, but the results would certainly make up for the effort such a crossing of disciplinary boundaries demands.

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